THE IMPORTANCE OF BEES AND OTHER INSECT POLLINATORS IN MAINTAINING FLORAL SPECIES COMPOSITION

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ABSTRACT.— Bees and other insect pollinators which are necessary for the successful reproduction of most species of flowering plants, including agricultural crops, have been ignored by our preservation efforts. This is unfortunate because bees, as low-fecundity natural organisms, are very susceptible to insecticides and populations are slow to recover from perturbations. Many species of bees, particularly specialized species in the western United States and the tropics, are vulnerable to extinction. With extinctions of specialized forms, generalized species, especially fugitives, are expected to increase because of their ability to utilize a variety of resources and survive beyond the confines of preserves. The possible effects of increased dominance by generalist pollinators on floral species composition is discussed.

Aside from being included in our objective to preserve existent natural diversity (Terborgh 1974), insect pollinators merit our preservation efforts because some 67 percent of extant flowering plants depend, to varying extents, upon them for reproduction (Axelrod 1960). Indeed, "pollinators are an environmental resource as critical to the long-term survival of a (plant) population as are light, moisture, etc." (Levin 1971). The adaptations for the attraction and utilization of insects by flowering plants for reproduction are impressive. They include size, color, fragrance, nectar, excess pollen, and nutrient contents, as well as morphology, positioning, and development of the floral parts (Percival 1965, Baker and Hurd 1968, Faegri and van der Pijl 1971, Leppik 1972, Proctor and Yeo 1973). In the absence of insects, most flowers as they are produced today would be maladaptive and our flora would assume a different aspect.

An example of a flora with few available pollinators is that of the Galapagos Islands, where only one species of bee and 19 species of lepidoptera have been recorded (Linsley 1966). Where pollinators are in extremely short supply it is disadvantageous to produce large, attractive flowers. Instead, we expect selection for wind pollination or autogamy with a concomitant reduction in conspicuous flowers (Rick 1966). In fact, there are few brightly colored flowers in the Galapagos; most are drab, and "endemics tend to have reduced corollas" (Rick 1966). In pollination tests with 18 species from seven families, Rick found a high incidence of autogamy: 13 species self-pollinated automatically and one was self-compatible. Results from four other species were inconclusive. Linsley et al. (1966) have speculated that successful invasion of the islands may have been restricted to those plant species which are either wind or self-pollinated or compatible with available pollinators. Thus, the Galapagos flora is probably less diverse than it might have been had the pollinator diversity been higher.

Bees are the most important of insect pollinators. Except for masarid wasps and a few beetles, only bees depend exclusively upon pollen and nectar for food throughout their life cycle. Their coevolution with flowering plants is manifest in the many morphological, behavioral, and physiological adaptations which make them more efficient at flower utilization (Linsley 1958, Percival 1965, Baker and Hurd 1968, Stephen et al. 1969, Faegri and van der Pijl 1971, Proctor and Yeo 1973).

In many cases the reciprocal adaptations between particular bee and plant taxa have

become rather specialized. Within the genus *Penstemon*, for example, species of the Series Graciles are adapted for pollination by bees of the genus *Osmia* (Crosswhite and Crosswhite 1966). Tropical orchids attract males of particular species of bees of the genus *Euglossa* by specific fragrances (Williams and Dodson 1972). *Pedicularis* species are pollinated only by bumble bees (e.g., Macior 1977). The pollen and nectar of the poisonous range plant death camas (*Zigadenus* spp.), though deadly to honeybees (Hitchcock 1959), are utilized by the oligolectic bee *Andrena astragali* Viereck & Cockerell, which also pollinates the plant (pers. obs.).

In addition to our native flora, many important agricultural crops, including cole crops, orchard fruits and nuts, bushberries, strawberries, some citrus fruits, sunflowers, cucurbits, alfalfa, and red clover either require insect pollinators for seed set or set more seed in their presence (Free 1970, McGregor 1976). Although most crop pollination is presently accomplished by honeybees, reports of native bees visiting flowers of agricultural crops are common (Free 1970, McGregor 1976), and endemics are undoubtedly responsible for some, as yet undetermined, percentage of crop pollinations. Two solitary species have replaced the honeybee as the preferred pollinator of alfalfa in the northwestern United States (Bohart 1972b), and another species, *Osmia lignaria* Say, shows considerable promise as a pollinator of pome crops (P. F. Torchio, pers. comm.). Native bees will probably play an especially important role in the pollination of sunflowers, a rapidly increasing native crop (F. D. Parker, pers. comm.). The preservation of exotic bees will be important as we increase our agricultural acreages of introduced crops and seek to import pollinators that have coevolved with those crops. For example, the primary pollinators of alfalfa in the northwest, *Megachile rotundata* (Linnaeus), is an exotic species native to Europe.

Of Grasshoppers and Bees

During the summer of 1978 a news release in the *Laramie Daily Boomerang* announced that a joint federal, state, and locally funded insecticide spray program would be con-

ducted in northeastern Wyoming to control grasshopper populations that had exceeded economically safe levels. I paraphrase the last segment of the news release: "Those who are concerned about bee populations in the area please note that all bees will be removed before spraying is conducted." This is quite an impressive feat considering that Wyoming has a minimum of 660 species (Lavigne and Tepedino 1976), all but one of which evolved with the native flora. The single exotic, *Apis mellifera*, the honeybee, was, of course, the species that was moved.

At the time insecticide was applied there were probably between 25 and 50 species of bees in the area. Unfortunately, no studies assessing the affect of spraying were undertaken, but other work has shown severe pollinator depletion following insecticide application (Kevan 1975, Plowright et al. 1978, Robinson and Johansen 1978). Because of their susceptibility to pesticides (Johansen 1977), wild bee populations were probably decimated.

The rate of recovery of an animal population whose numbers have been drastically trimmed is positively correlated with the intrinsic rate of increase of that population (May et al. 1974). Though females of many insect species produce hundreds or thousands of offspring, each of which receives little or no parental care, bees have developed a contrasting strategy. Bees produce few offspring and expend considerable effort to insure the survival of each. Greenhouse studies at the USDA Bee Biology and Systematics Laboratory with several solitary species, under conditions of excess bloom and without natural enemies, show that maximum fecundity averages 15–20 offspring per adult female. In the natural environment, where bloom is only occasionally superabundant and competitors, predators, and parasites abound, fecundity must be much lower. Because of their low fecundity, bees recover slowly from bouts of insecticide spraying or other perturbations. Plowright et al. (1978) estimated that three to four years would be necessary for bumble bee populations to return to prespray levels. Such estimates assume cessation of spraying and a continuously favorable environment. Periodic spraying or long periods of weather

unfavorable for flight would further slow re-covery rates.

The low fecundity of bees has other ef-fects. Smaller populations are more vulner-able to local extinction by random events (McArthur and Wilson 1967). If bee popu-lations are periodically or consistently dis-turbed, numbers will remain below carrying capacity for extended periods, and popu-lations will become more prone to random extinction. The resistance to insecticides de-veloped rapidly by many pest species is par-tially due to the great genetic variability con-tained in the prodigious numbers of offspring produced by single females (Georhgiou 1972). Because of reduced fecundity, bees may be less likely to develop resistance than other insect species. Indeed, resistance to in-secticides is unknown in bees.

The example of the bees that were not moved (or even considered) illustrates our philosophy of preservation. We have empha-sized the preservation of species that are "useful," closely related, or obvious to man. We overlook the functionally important or-ganisms that are frequently small and more subtle in their actions. For example, insects, the most influential of terrestrial animals (man aside), whether judged by numbers of species, individuals, or biomass, are repre-sented by only eight threatened and endan-gered species, all butterflies. Yet there are over one million described insect species and at least as many awaiting description. The base of the trophic pyramid, plants, are rep-resented by a mere 22 species. In com-parison, 588 species of vertebrates appear on the latest Threatened and Endangered Spe-cies List (U.S. Department of the Interior 1977). A trend is evident even within the class Vertebrata: 7.0 percent of all mammals are threatened or endangered, 2.5 percent of all birds, and 1.2 percent of all reptiles and amphibians—but only 0.3 percent of all fish. It is time that we attend to the preservation of functionally important organisms without backbones, many of which make vertebrate existence possible.

The Rarity of Bees

As pointed out by Bohart (1972a), the ef-fect of man on wild bees has been both posi-tive and negative. Overall, however, bee populations are probably in decline due to habitat destruction and to our increasing de-pendence on insecticides and herbicides. But even this assessment is tenuous because of the paucity of hard information. There are over 20,000 extant species of bees, and we know almost nothing of all but a handful of them. Our knowledge of tropical species is espe-cially poor, but we can guess that with man's rapid destruction of tropical habitats many species will be lost. Even in the western United States where bee diversity is very high (Linsley 1958) we do not know how many species, if any, have become extinct re-cently or how many may be threatened. In-deed, it is likely that the bee fauna of western North America harbors many undescribed species. For example, in two years of collec-ting on shortgrass prairie in southeastern Wyoming, I recorded over 200 species, 5–10 percent of which are new to science.

We do know from museum records that many species are rarely collected. Lists of such species could be compiled, but are these species truly rare (Drury 1974), or simply un-derrepresented in collections? Two of the many possible examples illustrate this prob-lem of identifying endangered bees. Until 1975, *Osmia tanneri* Sandhouse, a mason bee, was represented by a single male specimen collected in 1928 in the Raft River Moun-tains of Utah by Vasco M. Tanner. F. D. Parker (1975) rediscovered the species nest-ing near Wellsville, Utah, and in 1978 Tepe-dino and Boyce (submitted) found a large nest in a lawn in Laramie, Wyoming. Fifty years after the species was discovered we know little more than that it still exists and it builds mud nests under rocks.

The genus *Dufourea*, a ground-nesting group, provides numerous examples of spe-cies with restricted distributions. G. E. Bo-hart of the Logan Bee Laboratory is cur-rently studying the systematics of this group and has kindly furnished the following infor-mation. Over half of the 70 known species are restricted to California, and many of these have been recorded from only a single county. An undescribed species is restricted to the hills west of San Bruno, an area which is likely to undergo considerable devel-opment in the near future. Another undes-

cribed species is represented by two speci- mens collected in Joshua Tree National Monument. *Dufourea macswaini* Bohart has been collected only from the flowers of *Clarkia purpurea* in Madera County. Ten to fifteen other species have restricted, allopat- ric distributions on the west slope of the Sierras. With the continuing increase in pop- ulation and habitat destruction in California, it is likely that many of these rare species will disappear.

For a single region, Wyoming shortgrass prairie, we know that species abundance curves for bees show the typical insect pat- tern (Williams 1964): there are a few abun- dant species and many rare ones (Fig. 1). Some of this rarity is undoubtedly due to in- adequate sampling or to the capture of errant individuals which are abundant at higher ele- vations 5–10 km away. However, many of these species may be fugitives (see below), whose local abundance shows much spatio- temporal variability.

The Island Effect

With increasing loss of habitat, many plant and pollinator species will be confined to is- land preserves of restricted size surrounded by unsuitable areas. The number of species supportable will be determined by size of the preserve and the distance to other preserves, expressed through immigration and extinc- tion rates (MacArthur and Wilson 1967). Such "mainland island preserves" and their appropriate design have been the subject of much discussion (Diamond 1975, 1976, Wil- son and Willis 1975, Simberloff and Abele 1976, Whitcomb et al. 1976, Pickett and Thompson 1978), but, in general, preserves should be as large as possible so as to reduce the probability of extinction of resident spe- cies. Large size preserves become more im- portant as suitable surrounding habitat di- minishes, because immigration rate decreases with increasing distance from potential source areas.

The islandlike nature of preserves will also influence the kinds of plants and pollinators which can survive. Preliminary studies of the Galapagos and other islands (Carlquist 1974) suggest that a depauperate pollinator fauna restricts successful colonization to auto- gamous and anemophilous plant species and to those compatible with the pollinator fauna. On our size-restricted mainland islands the flora and fauna is, for the most part, al- ready present. The questions are: Which por- tion of the pollinator fauna is most vulner- able to extinction, which species or species types are most likely to recolonize, and how will this affect plant community composi- tion?

Plant community composition can be al- tered by differential changes in any of the numerous selective pressures that operate at each stage in the life cycle of component plant species (Harper 1977). Reduction in seed set, because of changes in the pollinator fauna, is but one way to alter the abundance of a given plant species. Nevertheless, polli- nation is a critical step in the production of the sporophyte generation. Other factors that affect the relative success of a plant species, and ultimately community composition itself, operate subsequent to pollination. If the gametophytes are not brought together, no other factor is important.

The effect of a change in the pollinator fauna on particular plant species will depend upon how specialized in pollinator require- ments a plant is and which species of pollina- tor(s) has been lost. Specialized species have long been thought to be less adaptable to changing conditions and therefore more vul- nerable to extinction (Rensch 1959). Recent evidence supports this idea (Drury 1974, Case 1975, Diamond 1975, Wilson and Willis 1975). A plant which has evolved with a spe- cific pollinator is doubly disadvantaged be- cause it may become endangered through di- rect means, e.g., habitat loss, or by dis- appearance of its pollinator. Specialized pol- linators are exposed to similar risks.

Certain specialized pollinator species will require large tracts of land for their survival. Traplining species (Janzen 1971), which may be abundant in the tropics, require large areas for successful foraging and probably would not survive on smaller preserves. Plant species dependent upon traplining pollinators for outcrossing are also vulnerable.

If floral production by the food plant of a specialized pollinator is spatiotemporally variable, then reserves of a size sufficient to incorporate such variability will be necessary
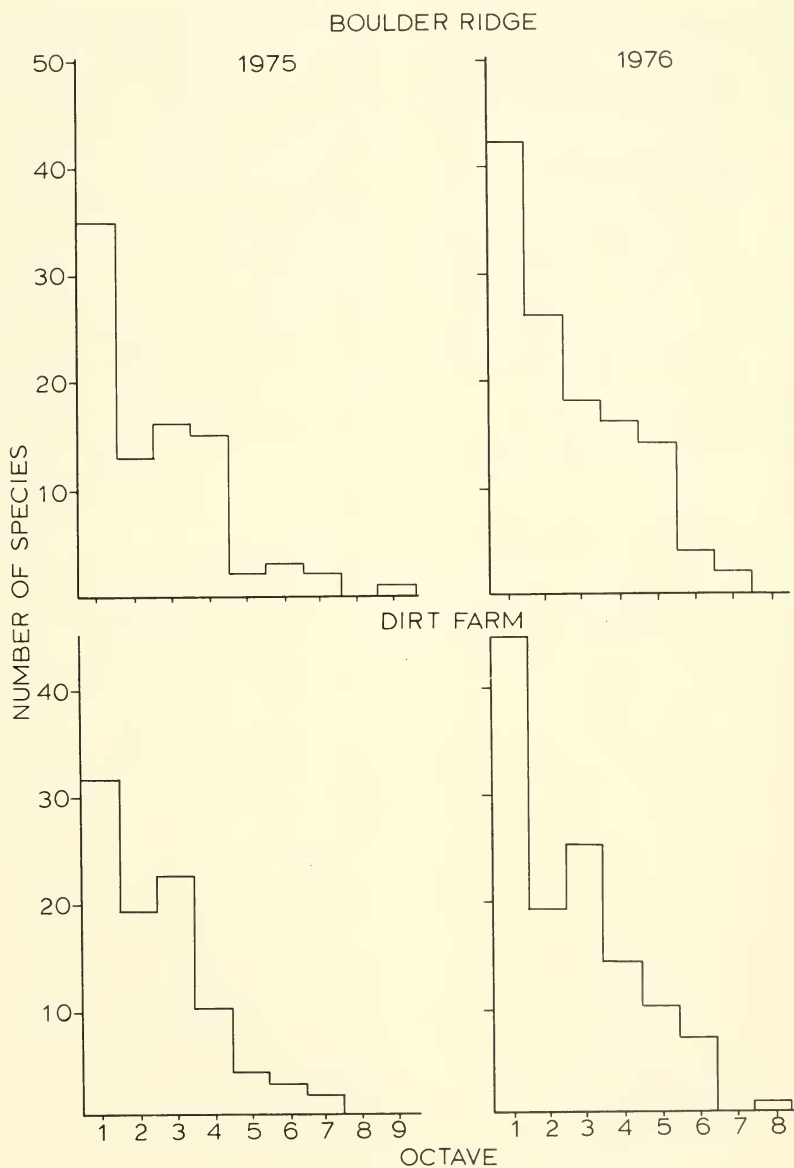
Fig. 1. Species abundance distributions for the bee fauna on two rangeland sites in southeastern Wyoming. Each site-year is treated separately. An octave is equivalent to $\log_2$ number of individuals. All curves, except Boulder Ridge 1975, fit a lognormal distribution.

if pollinator and plant are to be preserved. Little is known about variability in flower production between years in the same area or between areas within years. On shortgrass prairie, spatiotemporal variability in flower production is substantial (Tepedino and Stanton, in prep.). Other evidence from the literature tentatively suggests that many other regions exhibit similar variability between years in floral phenology (Tepedino and Stanton, in prep.) and that specialized plant species are no less variable than others (Tepedino and Sauer, unpubl. ms.). If we are to design natural reserves with necessary minimum dynamic area (Pickett and Thompson 1978) to accommodate pollinators, much additional data on variability of flower production by specialized plant species will be required. In general, however, smaller reserves are probably more stressful to specialist plants and pollinators than to generalized species.

Regions which harbor high proportions of specialized pollinators are especially prone to species loss. The Sonoran Desert, where Neff et al. (1977) estimated that 33–50 percent of bee species are specialized, is one such region. Indeed, much of the bee fauna of a substantial portion of the western United States, as well as other arid regions, may be specialized (Linsley 1958, Moldenke 1976). If specializations of euglossine bees are indicative of bee-plant relationships in the American tropics (Janzen 1971, Williams and Dodson 1972) then a substantial portion of the tropical flora and fauna may be jeopardized. Alternatively, the numerous species of stingless, social bees in the American Tropics, most of which are probably generalized in flower utilization, may indicate lower diversity of floral reproductive adaptations than we currently think. Many species of canopy trees, for example, produce large numbers of small, nonspecialized flowers (Frankie 1975) that superficially appear capable of utilizing a variety of insect species. We will need more data on tropical pollination systems before an adequate assessment can be made.

Most plant and pollinator taxa are not so specialized. For example, on Wyoming's shortgrass prairie most plant species are visited by many potential bee pollinators and most bee species utilize several flower species (Fig. 2). Moldenke (1975, 1976) reported similar results for several plant communities in the western United States. On shortgrass prairie, flower and pollinator usage also varied widely between years. Using Sorenson's presence-absence similarity index (Mueller-Dombois and Ellenberg 1974), we compared the plants foraged upon for each species of bee between years and, also, the pollinators which visited each species of plant in each year (Fig. 3). Most species of bees and plants were variable in their resource usage (low similarity values), especially at the Boulder Ridge site where floral variation was also greatest (Tepedino and Stanton, in prep.). Finally, most bee species also utilized a variety of flowers during particular foraging trips. Identification of pollen species from loads carried by bees showed that over 65 percent of all individuals had visited two or more plant species on a given trip and that 46 percent had visited more than three plant species.

Generalized bees are less vulnerable to extinction than specialists for reasons related to their ability to utilize a variety of flower species. First, unlike specialists, generalists will not become endangered because of the disappearance of a specific host plant. Second, the probability of a species becoming extinct due to random events increases with decreasing population size (MacArthur and Wilson 1967). Populations of resident generalists should be better buffered against wide fluctuations in numbers because of the wider potential resource base. In particular, population size of generalist species during unfavorable periods of bloom should be higher than that of specialists and therefore less prone to extinction. Finally, generalists are less dependent upon the size of preserves than specialists, because it is more likely that surrounding areas will contain plants which are suitable to them. In effect, the area suitable to generalists will almost always be greater than that for specialists and will extend beyond the confines of a preserve. Preserves should be designed with the minimum dynamic area (Pickett and Thompson 1978) necessary for specialist survival in mind.

One particular group of generalized bees that is least likely to be affected by habitat loss and disturbance is the fugitive species

contingent. Hutchinson (1951) proposed the term *fugitive* to describe species that avoid vying for limited resources with superior competitors by dispersing to localized patches of resource abundance where competition is temporarily relaxed. Fugitive bee species should be especially evident in habitats where floral resources are spatiotemporally unpredictable such as shortgrass prairie (Tepedino and Stanton, in prep.). Indeed, in these studies on shortgrass prairie, we found that less than 30 percent of the approx-
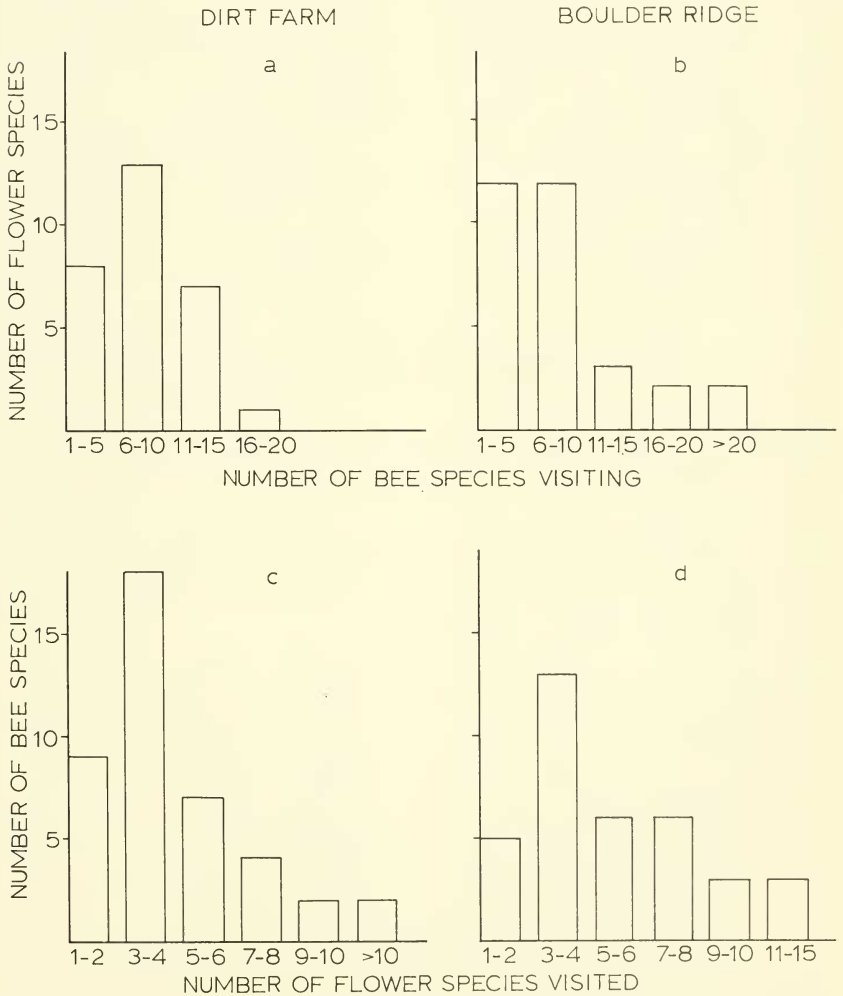

Fig. 2. a,b—Distribution of shortgrass prairie flower species according to the number of bee species visiting them over two years on two sites in southeastern Wyoming; c,d—distribuion of bee species by the number of flower species utilized.
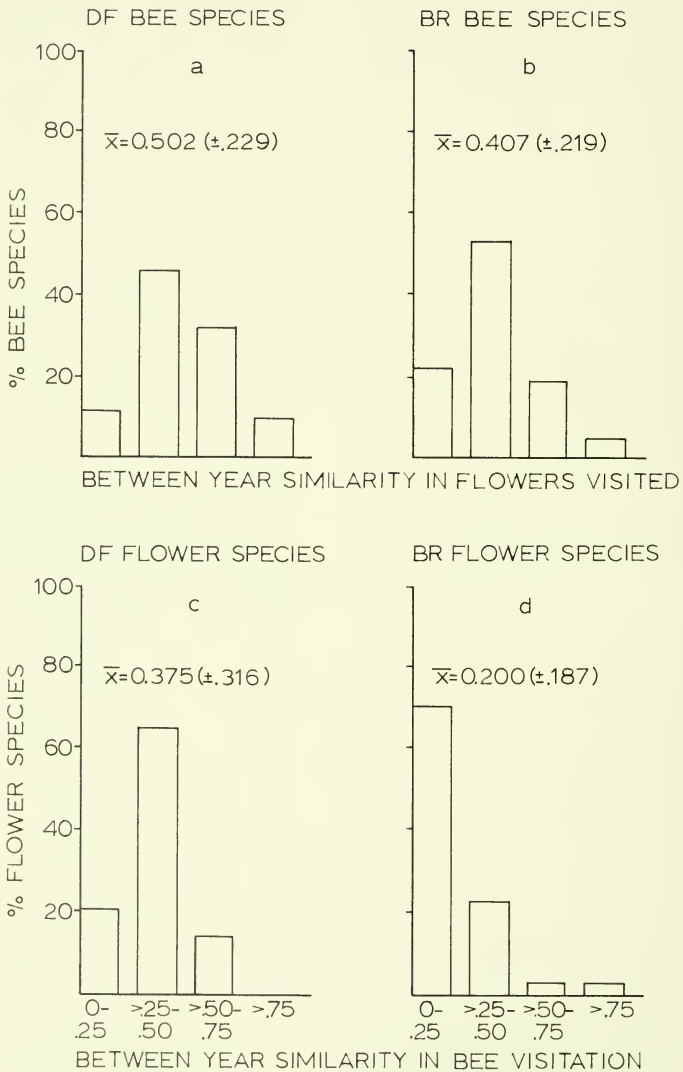
Fig. 3. a,b—Distribution of resident bee species by their similarity in flower utilization between consecutive years on two shortgrass prairie sites; c,d—distribution of flower species by their between-year similarity in bee species visiting them.

imately 150 bee species recorded on each of two sites could meet such relaxed requirements for residency as ≥ 3 individuals on a given site in each year. Most species were either present in very low numbers in each year or were abundant in one year and absent in the other. The percentages of total individuals collected that were nonresidents varied from 8.6–40.4 percent at the Boulder Ridge site and from 16.9–26.8 percent at the Dirt Farm. Although some nonresidents were undoubtedly incidentals from other habitats, the large number of species and individuals in this category suggest the presence of a substantial fugitive species contingent.

With diminution of native habitat, fugitive species will comprise an increasingly dominant element of the bee fauna. Unlike specialized bees and to a lesser extent resident generalists, fugitives will be uninfluenced by size of reserves because of their tendency to disperse and their ability to utilize a variety of floral resources. Fugitives will have little difficulty succeeding outside reserves because of the many patches of floral resources available along roadsides, in agricultural fields, backyards, etc. Indeed, these are the kinds of situations to which fugitives are adapted (Wilson and Willis 1975, Diamond 1976, Whitcomb et al. 1976). As resident bee species gradually disappear from reserves because of random extinctions of their relatively small populations, they will be replaced not by other immigrants of the same species but by fugitives.

The affect on the flora of losing generalized pollinators is difficult to assess. It is tempting to claim that many generalists are functionally redundant and therefore expendable; if lost, their pollinatory activities will be assumed by others. Such a justification for nonpreservation is potentially insidious because we have virtually no information on the relative efficiencies of different pollinators on particular plants or of a single pollinator on several plant species (Primack and Silander 1975). Conversely, several studies have now shown that plant and pollinator diversity are significantly correlated (Heithaus 1974, Moldenke 1975, del Moral and Standley 1979). A reduction in the diversity of either plants or pollinators may lead to a reduction in the diversity of the other.

There are reasons for believing that functional redundancy is minimal, and that elimination of generalized bee species as well as specialists can lead to differential alterations in seed set between plant species. First, some bees may collect nectar and/or pollen from certain species of flowers without pollinating them (Grant and Grant 1965, Faegri and van der Pijl 1971, Percival 1974, Tepedino 1975). Small species and certain bumble bees are more likely to fall into this "robber" category (Faegri and van der Pijl 1971). Their categorization as potential pollinators of those plants from which they rob is misleading and can lull us into a false sense of redundancy. We must be careful to distinguish between visitors and pollinators to arrive at intelligent conservation decisions, and this will necessitate much additional study. Nor is it valid to conclude that because a generalized pollinator robs the resources of one plant species it is without value as a pollinator of other species. Many bumble bees rob nectar from certain plants but are important pollinators of others (Faegri and van der Pijl 1971).

Secondly, although generalized bee species utilize a broader subset of available floral resources than do specialists, the foraging of any given species does not include all available flower species. Neither are the visits of any particular species proportional to the abundance of flower species available (Tepedino and Stanton, in prep.), nor are bee species equally efficient at pollinating all plant species visited. The extinction of a single pollinator species will reduce visitation rates to certain plant species in the community to some unknown degree. Without evidence, it seems overly optimistic to assume that such a reduction will be compensated for by remaining species. Further, even if visitation rates by other species do compensate for the lost pollinator, there is no basis for assuming that the efficiency of such visits is equivalent to that of the species which have disappeared. For example, in a study of four solitary bee species visiting alfalfa, Batra (1976) found that, although all gathered nectar and pollen and accomplished pollination, they did so with varying degrees of proficiency. Two species spent more time than others foraging on hidden flowers, one visited many more flowers which had already been

pollinated, etc. The species varied during morning foraging from 0.8 to 3.68 pollinations per minute. The effect of removal of one of these pollinators upon seed set would depend upon which species was removed. If we extend the results of this simple greenhouse study to plant communities in the field, we gain an impression of the unknown complexities which we are tampering with.

It seems clear that plant species that depend upon particular bees for their reproduction will experience severe selective pressures to evolve autogamy (Levin 1972) or wind pollination or to realign their floral morphologies to take advantage of remaining pollinator species. For many specialized plants such adaptations will be impossible (Levin 1971, Baker and Hurd 1968) and their extinction is likely. While it is not uncommon to develop facultative autogamy from obligate outcrossing (Baker 1959), selfing may be least advantageous in environments with low predictability such as shortgrass prairie (Solbrig 1976). In such regions plant species that solve pollination problems with obligate autogamy may become extinct more gradually.

As specialized pollinators are replaced by fugitives, more generalized plant species may become endangered because fugitives are relatively inconstant foragers. Several theoretical studies provide similar results for situations in which plant species compete for pollinator visits: if pollinator constancy is proportionate to floral abundance, minority species will receive fewer pollinating visits than more abundant species and will eventually disappear (Levin and Anderson 1970, Straw 1972, Waser 1978). Even worse, if pollinators show disproportionate preference for more abundant species, then less abundant species will approach extinction more rapidly.

There is little doubt that in North America we will lose many bee species and other pollinators as well, particularly from the western states. As a result of these extinctions, we will probably see some gradual transition in the composition of our flora. Floral change will be most obvious and far-reaching in desert, chaparral, and alpine ecosystems, where the percentage of insect-pollinated plants is high (Moldenke 1976). In forests and grasslands, where the dominant plant species are wind

pollinated, changes will be more subtle and less easy to predict.

Obviously, the key to slowing the rate of pollinator and plant extinction is habitat preservation. We need to set aside as much land as we can possibly afford in the form of greenbelts, parks, and reserves of various sizes. In addition, we should encourage the use of local plant species as ornamentals in backyards and gardens instead of the sterile creations of seed companies. Local plant species are frequently as esthetically pleasing and, because they are adapted to the region, require less care and expense in the form of fertilizers, water, etc. It is also quite simple to provide nesting material for some solitary bees in the form of pine wood blocks or scraps with holes drilled in them (Krombein 1967). These can be set out on posts in backyards as are bird houses and feeders. The species which will utilize these trap-nests are not at all agressive and will sting only when handled. In short, every little bit will help and, unfortunately, we need all the help we can get.

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